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Correlation of Variation between Leaf and Flower Characters in *Cymbidium goeringii* (Rchb. f.) Rchb. f. (*Orchidaceae*)

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We performed morphological and anatomical analyses to clarify the correlation of variation between leaves and floral characters of *Cymbidium goeringii* (Rchb. f.) Rchb. f. We observed that the morphological variation in leaf size was correlated with those of floral characters in this species. Moreover, the anatomical analyses indicated that the size variations in leaves, sepals, and petals were caused by decreased number of cells but those of the lips were caused by decreased cell number as well as decreased cell size. Various genes that do not participate in the formation of petals or sepals are involved in the development of the lip, suggesting that such genes contribute to specific processes related to the size variation of the lip at the cellular level.

Key words: allometry, anatomy, *Cymbidium*, *Cymbidium goeringii*, morphology.

Various studies on angiosperms indicate that in general, the size of branches, leaves, flowers, and inflorescences are allometrically related (White 1983, Primack 1987, Bond and Midgley 1988, Midgley and Bond 1989, Maitre and Midgley 1991, Kang and Primack 1999). In turn, this describes the correlation of variation between shape and size that can occur within a single type of organ or it can also involve the relative proportions of different organs (Huxley 1932). Such allometric growth is characterized by differential growth rates in different parts of an organism (Niklas 1994) and by changes in shape accompanied by changes in size (Brookstein 1991). For example, the correlation between plants and inflorescence size is attributed to pollinator visits (Donnelly et al. 1998, Elle and Carney 2003). Furthermore, it is suggested that pollinators come into contact with a greater number of flowers in plants with large inflorescences than those with small ones (Wilson and Price 1977). Moreover, if water conservation is promoted by small leaves and petals (McDonald et al. 2003, Galen 2006), selection could drive shifts in the sizes of both organs even if the underlying genes affect each organ independently. Developmental constraints provide another explanation (Maynard Smith

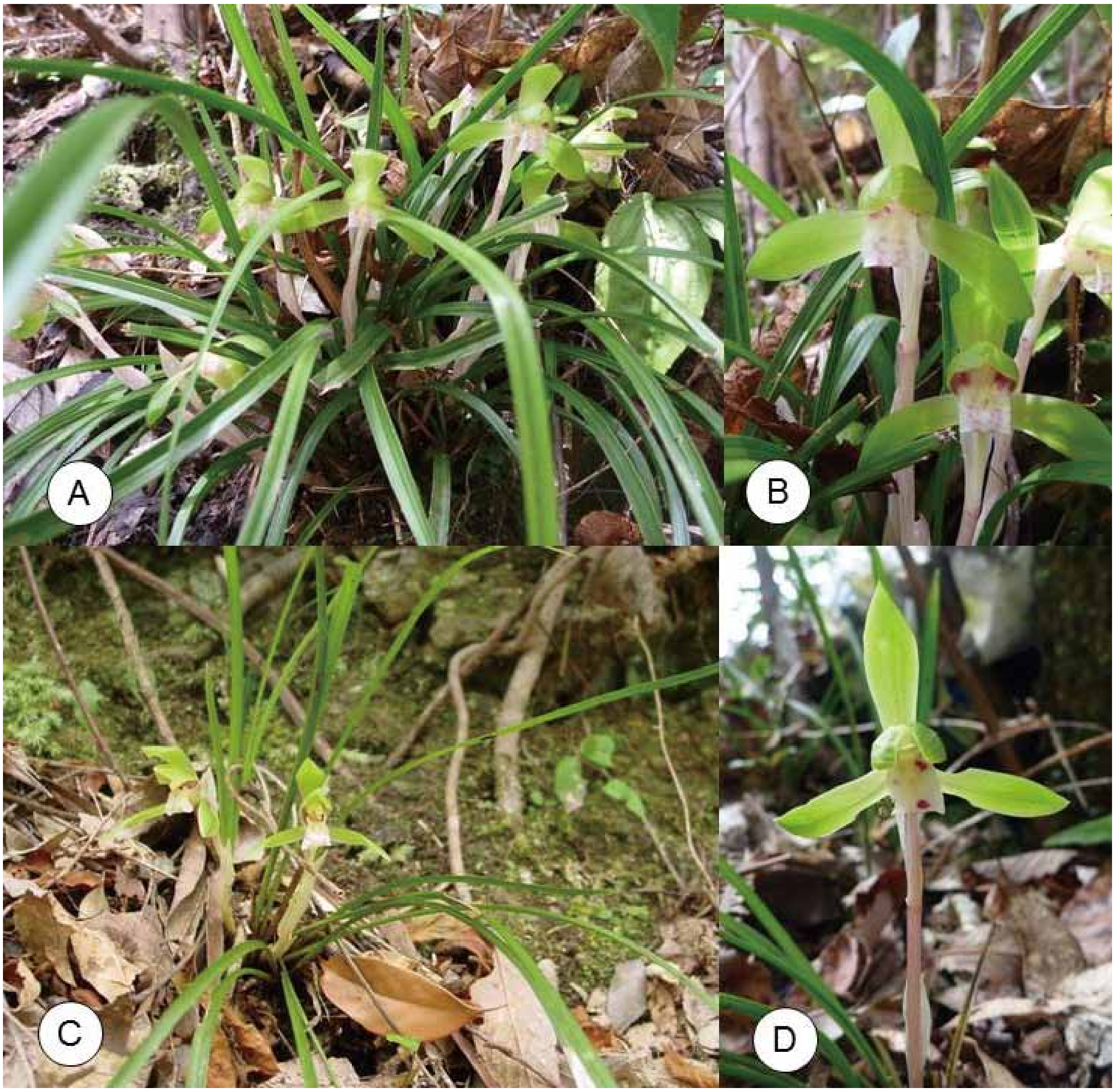

Fig. 1. *Cymbidium goeringii* var. *goeringii* (A–B) and var. *gracillimum* (C–D).

et al. 1985). For example, leaves and petals are homologous organs that share developmental control mechanisms (Anastasiou and Lenhard 2007) such that genes that act pleiotropically on both organ types might give rise to coordinated changes in shape or size.

With probably more than 20,000 species, orchids are unsurpassed by any other family in terms of their floral elaboration and diversity. Although the floral ground plan of orchids (i.e., the number and position of the structure elements) is very stable, it is variable with respect to vegetative architectures (Endress 1994, Johansen and Frederiksen 2002). Among orchids, *Cymbidium goeringii* (Rchb. f.) Rchb. f is distributed throughout Japan, Korea, China, and Taiwan (Figs. 1A, 1B) and includes infraspecific taxa that have varying vegetative characters. The stenophyllization of this species (2–3 mm width) is described as *C. goeringii* var. *gracillimum* (Fukuy.) T. S. Liu & H. J. Su and occurs in the eastern part of Kochi prefecture

Table 1. Sample of *Cymbidium goeringii* used in this study

	Locality	Sample size
I	Mt. Kunimi, Kagamiyoshiwara, Kochi City, Kochi Pref.	18
II	Mt. Kashiwao, Kohda, Kochi City, Kochi Pref.	5
III	Mt. Ohira, Tohzu, Kochi City, Kochi Pref.	11
IV	Mt. Tsukimi, Kishimoto, Kagami-cho, Konan City, Kochi Pref.	3
V	Ioki River, Aki City, Kochi Pref.	19 (4)
VI	Oshima, Kitagawa Village, Aki-gun, Kochi Pref.	4 (1)

Parenthesis indicate voucher specimens in Herbarium of Makino Botanical Garden, Kochi (MBK).

in Shikoku Island in Japan (Figs. 1C, 1D). Maekawa (1971) noted that this species tends to have a smaller flower size than *C. goeringii*. In fact, in our observations, both the leaves and floral characters of *C. goeringii* var. *gracillimum* appeared to be thin in Kochi prefecture. In this case, it is possible that the variation in leaf size between them is correlated with their floral characters. The objectives of this study are to clarify if there are morphological patterns and correlations among the structural parts of *C. goeringii*.

Materials and Methods

Plant materials

The samples of *Cymbidium goeringii* (including *C. goeringii* var. *gracillimum*) examined in this study were collected from the field and used from voucher specimens in the Herbarium of the Botanical Garden of Makino, Kochi (MBK). A total of 60 individuals representing six localities were sampled from both species (Table 1, Fig. 2).

Morphological analyses

For morphological analysis, the following characteristics of individual plants were measured: length and width of leaf blades; and floral components, including dorsal and lateral sepals, petals, lips, and peduncles. The measurements were obtained using a digital caliper; and micro-meter for thickness of leaf blades. Leaf measurements were obtained using fully expanded leaves.

Anatomical analyses

For anatomical analysis, fully expanded leaves and flowers were collected from each individual. To count the number of cells in the blade and flower, the surfaces of leaves and flowers were peeled off using Suzuki's Universal Micro-Printing (SUMP) method. The middle part of the blade along the midrib and the each floral component were analyzed to determine the number, length, and width of epidermal cells. The SUMP images of each leaf were examined five times for their floral components using a light microscope.

Results

Morphological measurements of Cymbidium goeringii

A summary of the leaf and flower measurements is provided in Table 2. The mean leaf width per plant was 6.64 (1.80) mm (range, 3.23–10.37 mm) (Fig. 3A). The leaf width per individual leaf ranged from 2.52 to 13.69 mm (Fig. 3B). The leaf length and thickness per plant were 32.07 (9.57) cm and 0.36 (0.06) µm, respectively. The leaf width had no significant relationship with either leaf length or thickness (r^2 = 0.011 and 0.142, respectively) (Figs. 4A, 4B).

The widths of dorsal and lateral sepals, petals, lips, and peduncles were 11.78 (1.16), 10.73 (1.17), 9.20 (0.67), 10.65 (0.94), and 3.86

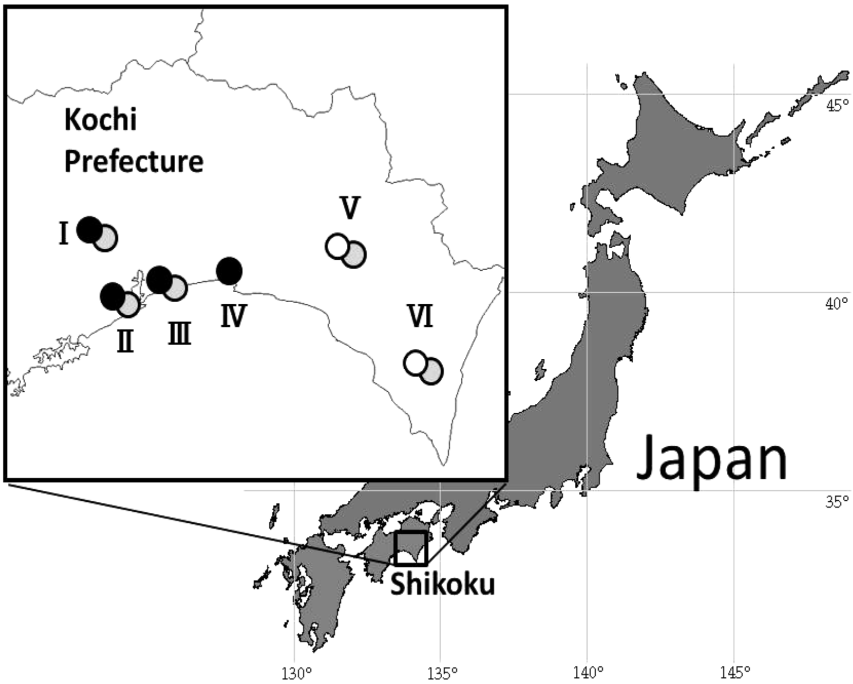

Fig. 2. Sampling localities used in this study. Open circles indicate narrow leaf widths (3–6 mm) of *Cymbidium goeringii*. Clouded circles indicate middle leaf widths (6–7.5 mm) of *C. goeringii*. Filled circles indicate wide leaf widths (7.5–10 mm) of *C. goeringii*. For other abbreviation, see Table 1.

(0.58) mm, respectively (Table 2). Regarding the relationships between leaf width and the widths of floral components, the leaf and sepal widths were significantly positively correlated ($r^2 = 0.372$**) (Fig. 5A). Moreover, leaf width was also significantly correlated with the widths of petals, lips, and peduncles ($r^2 = 0.522$**, 0.353**, and 0.420**, respectively) (Figs. 5B–5D).

Epidermal cells of Cymbidium goeringii

The width and length of the epidermal cells in the leaf were 16.68 μm (1.48) and 40.22 μm (4.69), respectively (Table 2, Fig. 6). Based on the widths and lengths of leaves and cells, we calculated the number of cells of a leaf to be approximately 410 (199) horizontally and 6968 (2069) longitudinally. We found a significant correlation between leaf width and the number of cells in the horizontal direction (Fig. 7A; $r^2 = 0.964$**). However, cell width did not exhibit any relationship with leaf width (Fig. 7B; $r^2 = 0.001$). We also found a similar trend regarding the longitudinal direction (Figs. 7C, 7D).

The widths and lengths (in μm) of epidermal cells of the following flower parts are as follows: dorsal sepals, 45.28 (4.38) and 71.02 (7.97); lateral sepals, 51.51 (7.02) and 62.77 (7.07); petals, 45.10 (4.95) and 68.92 (8.74); and lips, 62.39 (9.34) and 63.80 (10.00) (Table 2). Regarding the relationships between the widths of floral components and their cell numbers, the dorsal sepal width and its cell numbers were significantly positively correlated ($r^2 = 0.769$**) (Fig. 8A). Moreover, the other floral components (lateral sepals, petals, and lips) were also significantly correlated with their cell numbers ($r^2 = 0.643$**, 0.706**, and 0.339**, respectively) (Fig. 8B, C, and D). Of them, the trend of the regulation line and correlation coefficient

Table 2. Leaf and flower measurement in 60 specimens of *Cymbidium goeringii*

	Morphological measurements	Anatomical measurements		Relationship	
		Epidermal cell	Cell numbers		
	(A)	(B)	(C)	(A × B)	(A × C)
Leaf					
Length	32.99 (11.98)	40.22 (4.69)	6968 (2069)	n.s.	**
Width	6.95 (2.24)	16.68 (1.48)	410 (199)	n.s.	**
Thickness	0.38 (0.07)	—	—	—	—
Flower					
Dorsal sepal length	31.59 (2.34)	71.02 (7.97)	419 (53)	n.s.	n.s.
Dorsal sepal width	11.78 (1.16)	45.28 (4.38)	239 (46)	n.s.	**
Lateral sepal length	32.46 (2.45)	62.77 (7.07)	434 (83)	n.s.	n.s.
Lateral sepal width	10.73 (1.17)	51.51 (6.63)	184 (37)	n.s.	**
Petal length	25.01 (1.51)	68.92 (8.74)	395 (81)	n.s.	n.s.
Petal width	9.20 (0.67)	45.10 (4.95)	209 (39)	n.s.	**
Lip length	23.52 (1.17)	63.80 (10.00)	351 (52)	n.s.	n.s.
Lip width	10.65 (0.94)	62.39 (9.34)	160 (26)	**	**
Peduncle length	18.83 (3.15)	—	—	—	—
Peduncle width	3.86 (0.58)	—	—	—	—

Mean (standard deviation).
**: $P < 0.01$. *: $P < 0.05$. n.s.: $P > 0.05$.

between lip width and its cell numbers were low compared with other traits. On the other hand, the relationship between the lip width and lip cell width were significantly correlated ($r^2 = 0.284$**) (Fig. 9), even if the other floral components had no significant correlations between their widths and cell widths.

Discussion

Some studies of stenophyllization has been examined using anatomical and genetical analyses in rheophytic plants and a model plant, *Arabidopsis thaliana* (Tsukaya 2010, Setoguchi and Kajimura 2004). Stenophyllization in *Osmunda lancea* Thunb. appeared to be caused by a decrease in cell size to leaf-width (Imaichi and Kato 1992), however our results indicated that a decrease in the cell number of a leaf contributed to stenophyllization of *Cymbidium goeringii*, which is similar to previous anatomical studies of *Farfugium japonicum* (L. f.) Kitam. var. *luchuense* (Masam.) Kitam. (Nomura et al. 2006, Usukura et al. 1994) and *Rhododendron indicum* Sweet f. *otakumi* T. Yamaz. (Setoguchi and Kajimura 2004). Tsukaya (2002) indicated that variation in leaf width in the rheophyte *Dendranthema yoshinaganthum* (Makino ex Kitam.) Kitam. involved, for the most part, variation in the number of cells per leaf lamina. These results suggested that the decreasing cell numbers of a leaf might be a general tendency for stenophyllization in angiosperms.

One of the fundamental features of multicellular organisms is their ability to coordinate developmental processes at the tissue, organ, and organismal levels. Our results indicated that some organ characters exhibited significant correlations with each other (Fig. 5). This suggests that developmental constraints are involved in the correlated evolution of leaves, sepals, petals, and lips of *C. goeringii* rather than the selection of genes that affect them independently. In general, organ development is mediated by the temporal and spatial

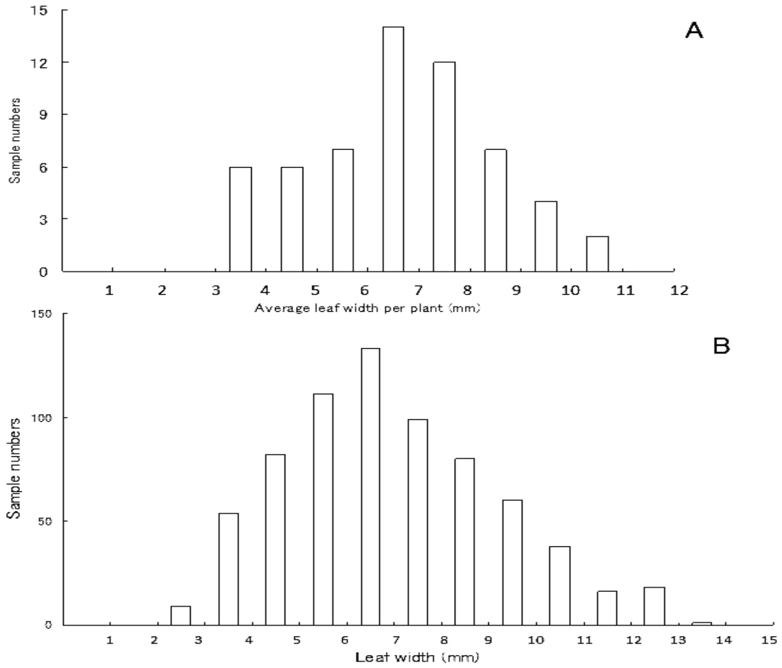

Fig. 3. Leaf width of *Cymbidium goeringii*. A. Average leaf width per plant. B. Leaf width per individual leaf.

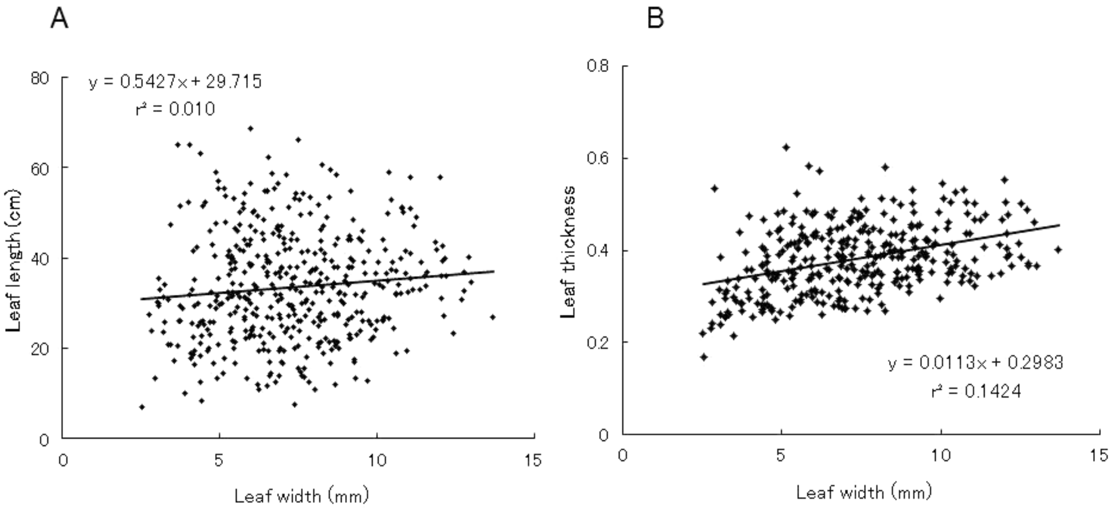

Fig. 4. Relationships between leaf width and length, and leaf width and thickness.

regulation of cell proliferation and expansion; therefore, we compared the cell numbers with the sizes of those organs. The results indicated that cell size is involved in the morphological variation of leaves, sepals, and petals but not lips (Fig. 7), suggesting that the variation in these organs of *C. goeringii* is a result of similar processes at the cellular level. In this case, it is possible there are genes to control leaf and floral characters. Virtually, all the research on

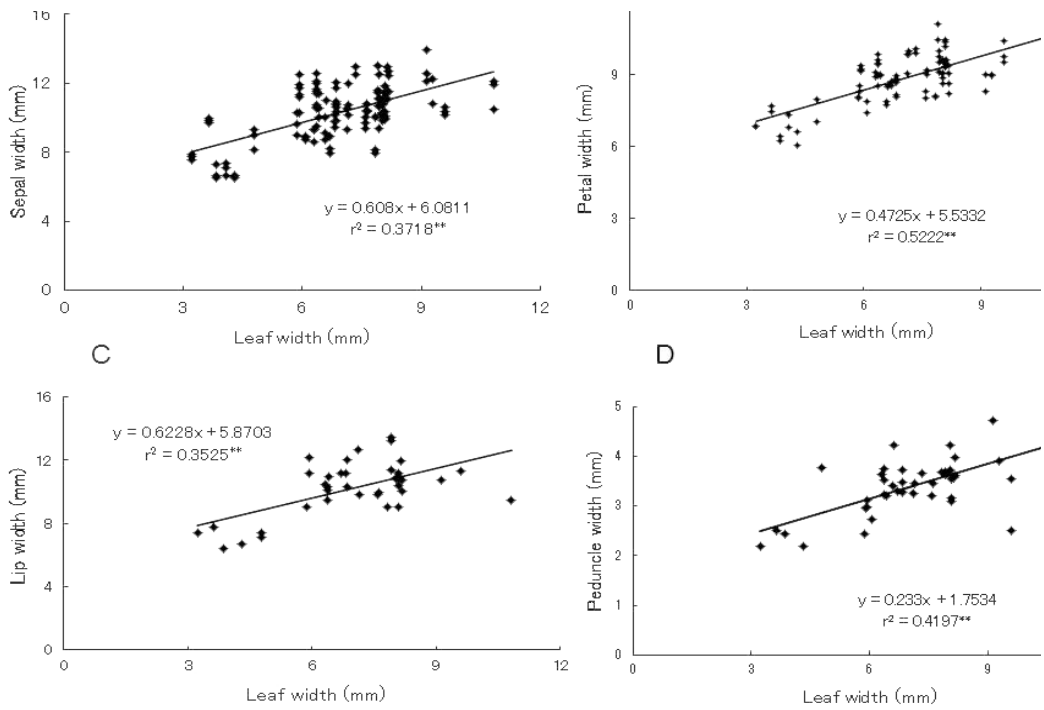

Fig. 5. Relationships between leaf width and floral components. A. Sepal width. B. Petal width. C. Lip width. D. Peduncle width.

the genetics of leaf and floral development utilizes mutagenesis to create loss-of-function mutations that dramatically alter organ size and shape. Using this approach, a number of major genes that cause gross abnormalities in leaf and floral development of some plant taxa have been identified and characterized (Bharathan and Sinha 2001, Kessler et al. 2001, Hareven et al. 1996, Pnueli et al. 1991, 1994a, 1994b, Dengler 1984). Considering these genetic and developmental results, it may be a general phenomenon that there is a correlation between the leaf and floral characters of *C. goeringii* at the cellular level.

The lip appears at the bottom of the flower and includes a nectary at its base where it forms an alighting platform for pollinators. Some pollinators enter the lip through the obvious large opening while others become trapped in the lip. It is considered that a change in lip size is accompanied by changes in pollinators. Therefore, our results suggest that the range of variation of lip size of *C. goeringii* could hardly be the result of any selection for pollinators. However, it is very interesting to note that there is no correlation between the sizes of lips and other organs, suggesting that the morphology of the lip is involved in different and/or developmental processes. In this case, it is questionable whether there is any genetic evidence to establish a relationship between lips and petals. For example, regarding lip development at the molecular level, Tsai et al. (2004, 2005) found that 5 MADS-box genes (*PeMADS2*, *PeMAD3, PeMAD4*, *PeMAD5*, and *PeMAD6*) played important roles in lip development in *Phalaenopsis*. Moreover, Song et al. (2006) reported that *PhalAG1* and *PhalAG2* were also involved in the development of lips of *Phalaenopsis*, suggesting that these genes lead to the formation of particular organs such as lips in orchids. Therefore, such genes

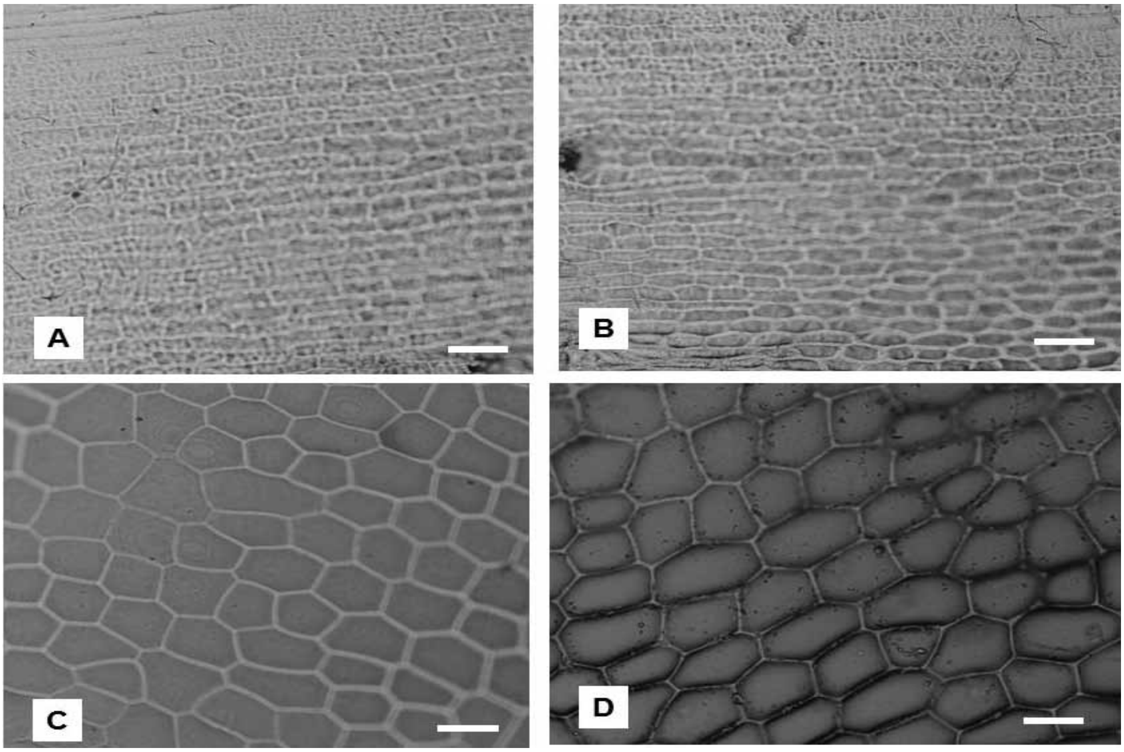

Fig. 6. SUMP replicas of *Cymbidium goeringii* var. *goeringii* and var. *gracillimum*. A. Leaf of *C. goeringii* var. *goeringii*. B. Leaf of *C. goeringii* var. *gracillimum*. C. Dorsal sepal of *C. goeringii* var. *goeringii*. D. Dorsal sepal of *C. goeringii* var. *gracillimum*. Bar = 50 μm

may contribute the size variation of lips in *C. goeringii*, which is specifically caused by cell number and size.

In this study, we indicated that the thinner leaf-type of *C. goeringii*, including *C. goeringii* var. *gracillimum* share sympatry in eastern Kochi prefecture in Shikoku Island in Japan. Sawa (1976) reports that this particular type of *C. goeringii* from various areas shifted towards having broader leaves under various cultivated conditions; however, one from eastern Kochi did not exhibit this tendency, indicating that it is the only population from this area to move towards the thinner leaf-type at the gene level. Moreover, the thinner leaf-type of *C. goeringii* was frequently found in eastern Kochi and its neighboring areas from our investigations of field and herbarium specimens (Fig. 2). From these results, we hypothesized that *C. goeringii* experienced hybridization and introgression with *C. goeringii* var. *gracillimum* in eastern Kochi. Various intergenic spacers have been widely analyzed to detect hybridization in wild plants (e.g., Soltis and Soltis 1998). Therefore, in future, molecular analyses using such samples are required to clarify our hypothesis.

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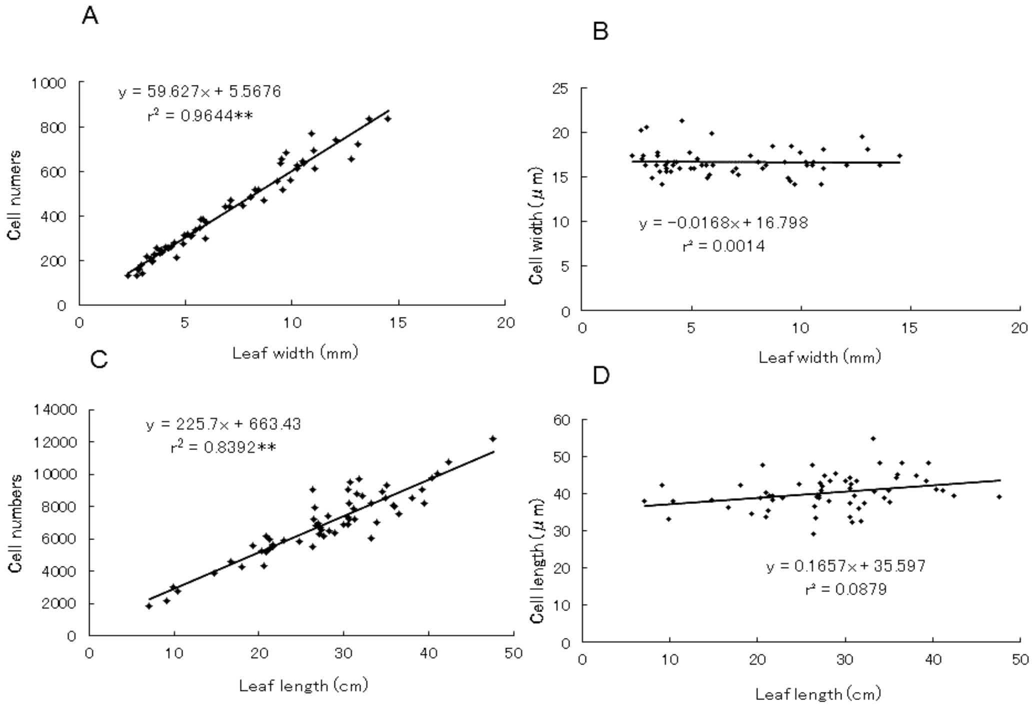

Fig. 7. Relationships between the width or length of leaf and their epidermal cell. A. Cell numbers in horizontally. B. Cell width in horizontally. C. Cell numbers in longitudinally. D. Cell width in horizontally in longitudinally.

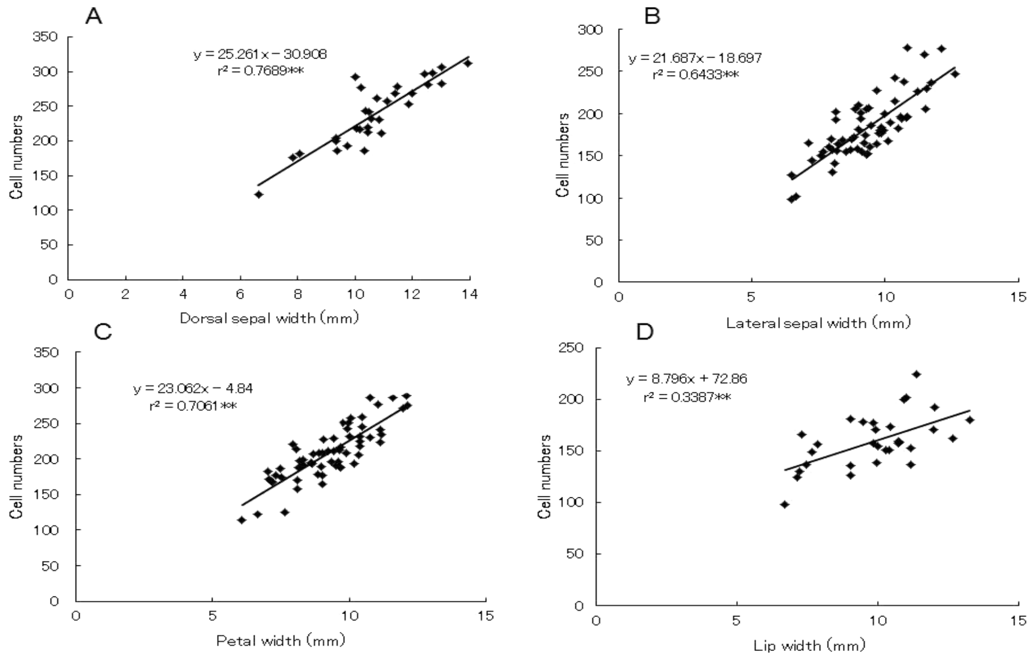

Fig. 8. Relationships between the widths of floral components and their epidermal cell number. A. Dorsal sepal. B. Lateral sepal. C. Petal width. D. Lip width.

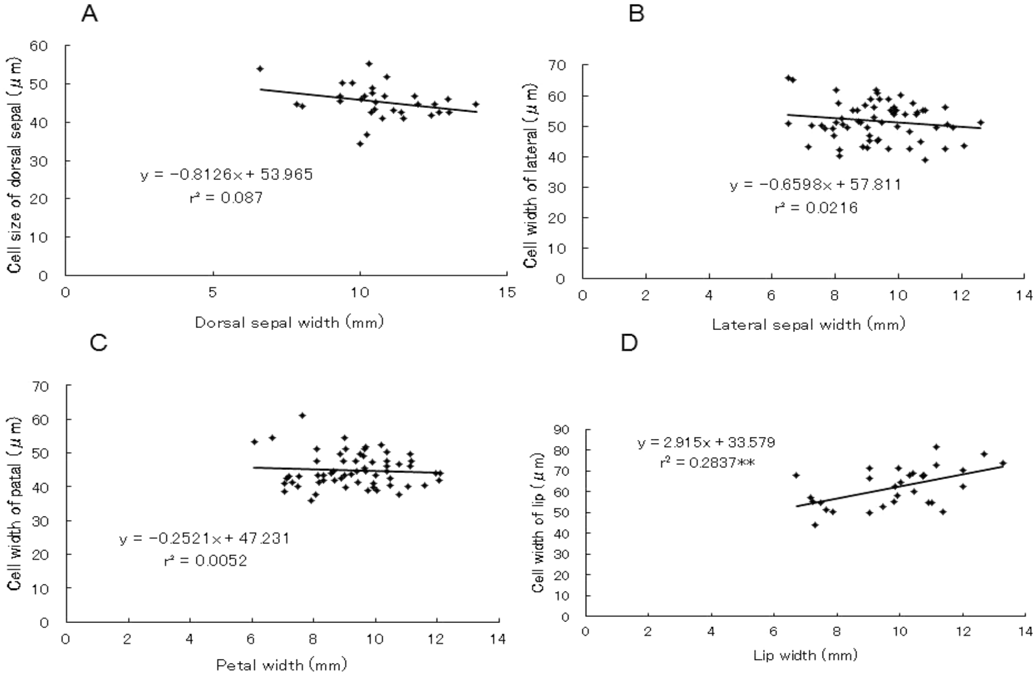

Fig. 9. Relationships between the widths of floral components and their epidermal cell width. A. Dorsal sepal. B. Lateral sepal. C. Petal width. D. Lip width.

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早川宗志[a,b]，室井美和子[c]，濱地秀徳[a]，横山 潤[d]，福田達哉[a,*]：**シュンランの葉と花における形態変異の相関関係**

シュンラン *Cymbidium goeringii* (Rchb. f.) Rchb. f. の葉と花における変異の関連性を明らかにするために，形態学的および解剖学的解析を行った．形態測定の結果，葉幅と花の各構成部位の幅の変異は相関していた．さらに，解剖学的解析より，葉幅，外花弁の幅，内花弁の幅の減少には細胞の数が減少し，唇弁の幅の減少は細胞の数とサイズの両者が減少していたことが明らかとなった．ランの唇弁の発達には外花弁と内花弁の形成に影響を与えないさまざまな遺伝子が関与しており，これらの遺伝子が細胞レベルで唇弁形成の特異的過程に関与していることが示唆された．

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